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Abstract
Anthropogenic water management projects and facilities that alter the local and regional hydrology of riverine environments greatly influence the behavior, physiology, and survival of native fishes. To mitigate for losses of native fishes at these structures, many are outfitted with fish-exclusion screens to reduce entrainment. The effect of fish size and age on behavior near fish screens, however, is largely unknown. Therefore, we tested two size classes of juvenile green sturgeon (*Acipenser medirostris*; small, early juveniles: 9.2 ± 0.2 cm fork length [FL], 6.9 ± 0.3 g; intermediate juveniles: 18.8 ± 0.2 cm FL, 36.9 ± 0.8 g) near fish-exclusion screens in a laboratory swimming flume. Although size was a significant factor influencing the way in which fish contacted the screens (i.e., proportion of body contacts, $p = 2.5\times10^{-9}$), it did not significantly influence the number of times fish contacted screens or the amount of time fish spent near screens. We also compared the performance of these two size classes to that of older and larger sturgeon that were tested previously (29.6 ± 0.2 cm FL, 147.1 ± 3.1 g), and documented a clear difference in the behavior of the fish that resulted in disparities in how the large fish contacted screens relative to small- or intermediate-sized juveniles ($p = 0.005$, 5.4×10^{-4}, respectively). Our results further our understanding of how ontogeny affects fish behavior near anthropogenic devices, and are informative for managers seeking to identify the most susceptible size and age class of juvenile green sturgeon to water-diversion structures to potentially develop size-specific conservation strategies.

Keywords: Ontogeny, Threatened species, Anthropogenic effects, Conservation, Rheotaxis, Swimming performance

Introduction

Freshwater fish populations worldwide are in decline (Moyle and Leidy 1992; Mallen-Cooper 1984; Dudgeon et al. 2006), particularly in areas where both anthropogenic stressors and climate change (Schindler 2001; Xenopoulos et al. 2005; Dudgeon et al. 2006) have led to habitat loss and degradation (Morita and Yamamoto 2002; Schrank and Rahel 2004; Mount et al. 2012), or changes in abiotic environmental variables (Marchetti and Moyle 2001; Wenger et al. 2011). In order to more effectively manage and conserve fishes, an understanding of physiological ecology and behavior is crucial, particularly for fishes with complex life history strategies. Indeed, a call for greater integration of physiological information with fisheries management has been made in recent years (Wikelski and Cooke 2006; Horodysky et al. 2015), and more state and federal agencies have recognized the need for a detailed understanding of fish physiology.

Size is an important aspect of physiology to consider when assessing the response of fishes to environmental variables or anthropogenic stressors (Kynard and Horgan Kynard et al. 2002; Nobriga et al. 2004; Komoroske et al. 2014). As fish grow and develop, behavioral and physiological responses to external stimuli may be altered or change entirely. In part, this can be due to the overall growth in absolute size, which can influence important physiological and ecological processes, such as swimming performance (Peake et al. 1997; Allen et al. 2006; Verhille et al. 2014), predation risk (Lundvall et al. 1999; Gadomski and Parsley 2005) and foraging behavior (Werner and Hall 1988), among others. Additionally, size can indirectly affect physiological or behavior responses in fishes due to differences in the requirements for distinct life history stages (Folmar and Dickhoff 1980; Veselov et al. 1998; Allen and Cech 2007). For example, as anadromous fishes transition from one life history stage to the next, unique physiological or behavioral characteristics are expressed, and are often accompanied by changes in habitat selection (Hoar 1988; Quinn and Myers 2004). The parr and smolt stages characteristic of most Pacific salmonid species each have distinct morphological, physiological and behavioral traits: parr are well equipped to live and survive in freshwater environments, while the process of smoltification mediates a transition to residence in seawater (Folmar and Dickhoff 1980); including a change in rheotactic behavior that promotes downstream movement. As such, understanding how size can modify the behavioral and physiological responses to environmental or anthropogenic stressors is an important component to consider when developing conservation and management strategies.

Green sturgeon are a long-lived species of important conservation and management concern in the state of California (NMFS 2006; Israel and Klimley Israel and Kimley 2008; Klimley et al. 2015). They are fully anadromous (Doroshov 1985; Allen and Cech 2007), which underscores the importance of considering the early life history stages of this species when implementing management or mitigation projects. After emergence and the development of exogenous feeding (ca. 15 days post hatch [dph], 1 g, 3 cm fork length [FL] at 18 °C; Van Eenennaam et al. 2001), larval fish remain in the upper reaches of freshwater rivers until completion of larval development into juveniles (ca. 60 dph, 7 g, 10 cm FL at 18 °C; Van Eenennaam et al. 2001). Juvenile green sturgeon remain in freshwater until they undergo a "pseudo-smoltification," during which their physiology is remodeled to tolerate salt water (Allen et al. 2009, 2011), and their swimming performance decreases to facilitate an outmigration from riverine environments (Allen et al. 2006), but which does not result in major morphological modifications as in salmonids. The timing of this outmigration is not well understood, but laboratory experiments have shown that juvenile green sturgeon can tolerate full-strength salt water by 134 dph (ca. 80 g, 20 cm FL at 19 °C; Allen et al. 2011). Similarly, pectoral fin ray microchemistry analyses performed on wild green sturgeon suggest that the transition from fresh water into areas with moderate salinity (i.e., an estuary) can occur as early as 6 months of age (~180 dph; Allen et al. 2009). As green sturgeon develop from early- to intermediate-stage juveniles (ca. 10 cm to ca. 20 cm FL), the changes in physiology and behavior, such as rheotactic behavior, that accompany the transition between life history changes are crucial to understand. Quantifying the behavior of a wide range of juvenile sizes that may encounter water diversions throughout the Sacramento-San Joaquin watershed prior to full outmigration is important, as green sturgeon juveniles may respond differently to anthropogenic stressors as they age. For long-lived species such as sturgeon, which do not reach sexual maturity until between 12 and 18 years of age (Doroshov 1985), recruitment failure of early life history stages has been suggested as a reason for population declines (Hardy and Litvak 2004), and conservation of juveniles is therefore crucial for long-term population stability.

Green sturgeon are native to the Pacific coast of North America, and have two distinct population segments (DPS; Israel et al. 2004); the Northern DPS spawns primarily in the Rogue and Klamath Rivers (Erickson et al. 2002), while the Southern DPS spawns only in the Sacramento-San Joaquin watershed in the Central Valley of California (Israel et al. 2004; Seesholtz et al. 2015). As with many rivers worldwide, the

Sacramento-San Joaquin watershed is a highly-altered ecosystem that is heavily modified by man-made structures such as dams, water pumping facilities, and water diversions (CDWR 2014). Over 3000 water diversions exist in the Sacramento-San Joaquin watershed (Herren and Kawasaki 2001), and roughly 40%of the water flow in the Sacramento River is diverted for urban and agricultural use (CDWR 2014). These water diversions pose a mortality or injury risk to migrating and resident fishes (Swanson et al. 2004, 2005; Young et al. 2010), and green sturgeon are particularly susceptible to entrainment into these structures (Mussen et al. 2014; Poletto et al. 2014b; Poletto et al. 2015).

To reduce the risk of entrainment, many water diversions are fitted with fish protection devices such as fish-exclusion screens that function as positive barriers which physically prevent fish from entering a water diversion (Taft 2000). The effect of fish screens on the behavior and physiology of fishes has been studied in the laboratory and the field (e.g., Boys et al. 2013a, 2013b; Swanson et al. 2004, 2005; Young et al. 2010), but few studies have focused on understanding interactions of sturgeon species with fish screens. A previous laboratory study on green and white sturgeon (*A. transmontanus*) behavior near fish screens showed that green sturgeon are susceptible to multiple physical encounters with fish screens, and can become impinged on screen faces (Poletto et al. 2014a). Repeated contact with or impingement upon fish screens has been shown to reduce swimming performance and increase predation risk in fishes, possibly because of increased physiological stress, exhaustion and metabolic disturbance elicited during escape attempts and physical damage from screens (Swanson et al. 2004, 2005; Young et al. 2010). As such, non-physical barriers such as sensory deterrents (Noatch and Suski 2012) are often coupled with fish-exclusion screens to further prevent potentially deleterious effects from encounters with the screens themselves. Common sensory deterrents include strobe lights, bubble curtains, or auditory and mechanical stimuli (Noatch and Suski 2012), though the efficacy of these barriers are often highly species-specific and context dependent (Poletto et al. 2014a).

Because several physiological performance metrics (such as swimming performance and metabolic rate) are influenced by size, it is important to quantify the behavioral responses of juvenile sturgeon to fish screens across a range of sizes and ages. Therefore, our objectives for this study were to 1) quantify and compare the behavior of two size classes of juvenile green sturgeon (small and intermediate juveniles) near fish screens in the laboratory, 2) assess the influence of non-physical barriers on the behavior juveniles near fish screens, and 3) compare these data

to previously-published data for larger green sturgeon juveniles. We hypothesized that small- and intermediate-sized juveniles would behave differently in the presence of fish screens, and would also differ from the behavior exhibited by larger juveniles in a previous study, but that the influence of nonphysical barriers on behavior would be consistent across size classes. These analyses will not only yield information that can be used by fisheries managers to develop life-stage specific management actions, but will also provide crucial insight on how behavior and physiology change as juveniles grow.

Materials and methods

Study species

Green sturgeon broodstock (northern DPS) were spawned at the UC Davis Center for Aquatic Biology and Aquaculture (CABA) in February and March 2010 (methodology described in Van Eenennaam et al. 2001) and reared at 18 °C in 815-l round fiberglass tanks with continuous flows of aerated, non-chlorinated fresh water from a dedicated well. Fish were fed daily to satiation with semi-moist pellets (Rangen, Inc., Buhl, Idaho; 17.9 MJ/kg) and eventually weaned onto a dry pelleted diet (SilverCup™; 16.6 MJ/kg) at ca. 60 days post-hatch (dph). All handling, care and experimental procedures used were reviewed and approved by the UC Davis Institutional Animal Care and Use Committee (IACUC #17017).

Flume and sensory Deterrents

Experiments were performed in an elliptical, indoor, flow-through, fiberglass swimming flume (1 m wide channel, 30 cm water depth) that allowed for flume water velocity control via a variable-frequency pump. Two wedge-wire stainless steel screens (1 m × 1 m, 2-mm bar spacing) were placed in a 60° V-configuration in the flume with the apex of the V pointed downstream. A stainless steel screen (wire-mesh 0.635 cm^2) was positioned 1.5 m upstream from the apex of the wedge-wire screens, to create an enclosed testing area in which fish were placed. Water temperature was maintained at 18 °C. For additional flume specifications see Poletto et al. (2014a).

To test the efficacy of commonly-used deterrents designed to reduce fish interactions with diversion screens, a strobe light (Monarch Instruments, DB Plus) was positioned above the flume to direct light onto the

screen faces, and pneumatically-operated vibrators (NTK25 Netter Vibrations, Model 55252) were affixed to each wedge-wire screen above the surface of the water. The strobe light was operated at 300 flashes per minute (FPM) and the wedge-wire screens were driven to vibrate at a frequency of 10 Hz, with only one of the two screens vibrating during an experiment. These rates were chosen to allow for direct comparison with previously published data investigating the effects of sensory deterrents on behavior in green and white sturgeon (Poletto et al. 2014a).

Experimental design

Two age and size classes of green sturgeon were tested: small- and intermediate-sized juveniles. Small juveniles from the February 2010 spawn (n = 89) were 53-79 dph, 9.2 ± 0.2 cm in fork length (FL), and weighed 6.9 ± 0.3 g. Intermediate juveniles from the March 2010 spawn (n = 137) were 115-152 dph, 18.8 ± 0.2 cm in FL, and weighed 36.9 ± 0.8 g.

For direct comparison of small and intermediate juvenile behavior with previously published data on larger green sturgeon behavior, experimental methodology followed that of Poletto et al. (2014a). Prior to each experiment, a group of ten randomly chosen juvenile green sturgeon were transferred from their rearing tank to a single indoor holding tank (140-l) located next to the experimental flume, to minimize handling stress. For each experiment, individual fish were removed from the holding tank and placed into the testing area of the flume for a period of 5 min without water flow or any stimulus presentation. This acclimation period allowed the fish to explore the testing area without any additional stimuli. Immediately following the acclimation period, a treatment condition, including water velocity, was induced, starting the experimental period. Fish were exposed to the treatment condition for 15 min. Fish were visually observed during each experiment, and if a fish became impinged on a screen (having >2/3rd of its body pinned against the screen face) for ≥30 s in a manner where the fish was unable to free itself from the screen, the experiment was terminated, and not included in subsequent analyses.

Experiments included the following treatment conditions, conducted at one water velocity (21.3 ± 0.1 $cm \cdot s^{-1}$, mean ± S.E.): control (no stimulus), strobe light, screen vibration (one screen only, randomly chosen), or a strobe light and screen vibration combination (where only one screen was randomly chosen to vibrate). These experiments were performed during the day under normal light conditions, and treatments were randomized. Experiments were recorded using a video camera (Sony DCR

DVD-505) mounted directly over the testing area. Following each experiment, the fish was removed from the flume and measured for length (fork length [FL], cm) and mass (g). Each fish was used only once, eliminating the possibility for fish to modify their behavior based on previous experience.

Three behavioral indices were quantified for the 15-min experimental period for each fish: the total number of screen contacts (both tail and body contacts), the proportion of contacts made by the body or tail, and the amount of time spent near screens (area within the 60° angle created by screen configuration) or upstream of the screens (area upstream of the 60° angle created by screen configuration; residence time, min). Body and tail contacts were counted as any physical contact the fish made with a screen. The proportion of contacts made by a fish with its body or tail is reported as the proportion of body contacts relative to total contacts (proportion of body contacts); frequency of tail contacts is therefore: 1 – proportion of body contacts. Residence time is reported as the proportion of time a fish spent near screens relative to upstream of the screens (time near screens); time spent upstream of screens is therefore: 1 – time near screens.

Data analysis

Data were analyzed using R Studio version 2.15.2 software (Development Core Team 2012) and the *car* (Fox and Weisberg 2011), *plyr* (Wickham 2011), *PMCMR* (Pohlert 2014), and *multcomp* (Hothorn et al. 2008) packages, while data were visualized using *ggplot2* (Wickham 2009). Total screen contacts were log transformed using the equation: $\log_{10}$(Total contacts + 1) to normalize the data and meet the assumptions of homoscedasticity, and were analyzed using a generalized linear model (GLM) with a Gaussian distribution. Statistical significance is reported for analyses performed on log-transformed data, while untransformed means are reported and described, due to the ecological relevance and management implications of these values. The proportion of body contacts and time spent near screens were both analyzed using GLMs with quasibinomial distributions. To avoid an artificial reduction in the proportion of body contacts, fish that made zero overall screen contacts (n, small juveniles = 5; n, intermediate juveniles = 7) were excluded from this analysis. All response variables were analyzed by assessing the significance of the categorical variables size class (small or intermediate), treatment (control, strobe light, screen vibration, or strobe light and vibration combination), and the interaction between the two, as determined

a priori. Model fit was evaluated graphically and tested against a null model. Post-hoc analyses on significant effects of size for each treatment were compared using Mann-Whitney rank sum tests. Posthoc analyses on significant effects of treatment were compared with multiple comparisons of means with single-step adjusted *p*-values using the *multcomp* package (Hothorn et al. 2008). Impingements were not analyzed statistically and will not be reported due to the low frequency of occurrence. Significance was considered at $\alpha \leq 0.05$.

To test the effect of size and ontogeny over a greater variety of sizes and ages, data obtained in this study were compared to previously published data on larger juvenile green sturgeon (age 150–198 dph) with a FL of 29.6 ± 0.2 cm and a mass of 147.1 ± 3.1 g (Poletto et al. 2014a). Importantly, the inclusion of these data allow us to quantify the behavior of a wide range of juvenile sizes that may encounter water diversions throughout the Sacramento-San Joaquin watershed before full outmigration. For these comparisons, only data obtained from fish tested under control conditions were used to reduce the variation associated with potential treatment effects. Data from larger juveniles are directly comparable to those obtained in the current study, because the fish were reared with identical protocols, and the control conditions, including water temperature, water depth and velocity were the same. All data were compiled and analyzed in R Studio using the packages described above. To first test the effect of size class on behavior, a Kruskal-Wallis one-way ANOVA on ranks with subsequent pairwise multiple comparisons of means was performed on each response variable, with size class as a categorical predictor variable (small, intermediate, large). To further investigate the effect of size on behavior, GLMs were then performed to analyze response variables (total contacts, proportion of body contacts, and time spent near screens) as a function of the continuous variable FL. Both linear and logistic models as a function of FL were assessed for each variable; the best-fitting model was chosen by selecting the one with the lowest mean residual error and confirmed by log-likelihood ratio tests. In the case of a non-significant log-likelihood ratio test, the simplest model was considered the best-fitting model. Total contacts were log transformed as described above, and analyzed using a Gaussian distribution, while the proportion of body contacts and time spent near screens were analyzed using quasibinominal distributions. Significance was considered at $\alpha \leq 0.05$.

Results

Total screen contacts

The total numbers of screen contacts for each deterrent treatment for both small and intermediate juveniles are listed in Table 1. Overall, smaller fish screen contacts were statistically indistinguishable from those of the intermediate-sized fish (29.6 ± 3.5, mean ± SE vs. 32.4 ± 3.4; $F_{1,225} = 0.18$, $p = 0.69$). Similarly, treatment did not have a significant main effect on screen contacts ($F_{3,225} = 0.21$, $p = 0.89$), and the interaction between size class and treatment was also non-significant ($F_{3,225} = 1.95$, $p = 0.12$). Also, screen contacts for both sizes of fish under control conditions were statistically indistinguishable from those under strobe light, vibrations, or strobe light and vibrations combination conditions (Table 1).

Proportion of body contacts

The proportion of screen contacts fish made with their bodies is shown in Fig. 1 for both small and intermediate juveniles. The effect of size class on body screen contacts was highly significant ($F_{1,213} = 38.9$, $p = 2.5 \times 10^{-9}$), though the effect of treatment and the interaction between the two were both statistically indistinguishable ($F_{3,213} = 0.40$, $p = 0.76$; $F_{3,213} = 0.79$, 0.50, respectively). Small-sized juveniles contacted the screens more often with their bodies (overall proportion of body contacts: 0.49 ± 0.03), while intermediate-sized fish contacted the screens more often with their tails (proportion of body contacts: 0.27 ± 0.02). Similarly, small-sized juveniles contacted screens more often ($p < 0.05$) with their bodies for all treatments except for the strobe light and vibration combination treatment ($p = 0.07$; Fig. 1).

Table 1. The mean (± SE) total number of small or intermediate juvenile green sturgeon screen contacts and proportion of time spent near screens (residence time) per 15-min treatment condition.

	Total screen contacts				*Residence time*			
Treatment	*Small*	*n*	*Intermediate*	*n*	*Small*	*n*	*Intermediate*	*n*
Control	44.2 ± 10.4	17	32.5 ± 8.1	28	0.41 ± 0.08	17	0.27 ± 0.07	28
Strobe Light	24.7 ± 7.1	17	43.7 ± 8.8	27	0.26 ± 0.07	17	0.43 ± 0.08	27
Screen Vibrations	25.4 ± 4.6	36	28.5 ± 5.3	54	0.19 ± 0.04	36	0.18 ± 0.03	54
Strobe Light + Vibrations	29.1 ± 7.4	19	29.1 ± 5.0	28	0.19 ± 0.06	19	0.29 ± 0.06	28

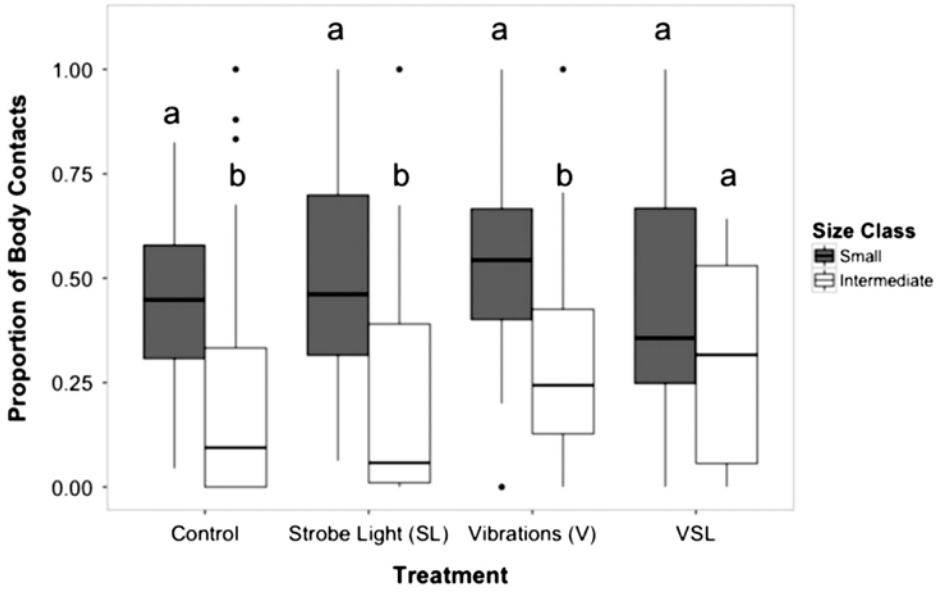

Fig. 1. The proportion of body contacts for small- and intermediate-sized juvenile green sturgeon. Significant differences between size classes for each treatment are indicated by different lowercase letters. Black line = median, box = interquartile range (IQ), whiskers = 1.5 IQ, closed circles = outliers. VSL Combination = vibration and strobe light combination.

Residence time

All fish spent a greater amount of time during the experiment upstream of the screens than near the screens, resulting in a proportion of time spent near screens of <0.5. Size class did not significantly affect residence time ($F_{3,225} = 0.36$, $p = 0.55$), as intermediate and small-sized individuals spent similar proportions of time near the fish screens (0.27 ± 0.03 vs. 0.24 ± 0.03, respectively). Overall, treatment had a significant effect on time spent near screens ($F_{3,225} = 4.15$, $p < 0.01$); posthoc analyses, however, did not reveal any significant differences between pairwise comparisons among treatments ($p > 0.05$ for all comparisons). The interaction between size class and treatment also did not significantly affect the proportion of time spent near screens (Table 1; $F_{3,225} = 1.81$, $p = 0.15$).

Comparison to behavior of larger juveniles

A comparison of large, intermediate, and small juveniles under control conditions is presented in Table 2. Size class had a significant effect on the total number of screen contacts ($\chi^2 = 9.49$, df = 2, $p = 0.009$), with

Table 2. A comparison of green sturgeon screen contacts, proportion of body contacts, and residence time among the three juvenile size classes, under control conditions.

			Control Treatment				
Size class	*Fork length (cm)*	*Mass (g)*	*Total screen contacts*	*Proportion of body contacts*	*Residence time*	*n*	*Experiment*
Small	9.2 ± 0.2	6.9 ± 0.3	44.2 ± 10.4ab	0.43 ± 0.06a	0.41 ± 0.08a	50	This study
Intermediate	18.8 ± 0.2	36.9 ± 0.8	32.5 ± 8.1a	0.25 ± 0.06a	0.27 ± 0.07a	81	This study
Large	29.6 ± 0.2	147.1 ± 3.1	58.3 ± 7.0b	0.83 ± 0.03b	0.31 ± 0.08a	54	Poletto et al. (2014a)

Different lowercase letters represent statistical differences among size classes for each response variable.

large individuals contacting the fish screens a significantly greater number of times than intermediate-sized fish ($p < 0.01$; all other comparisons $p > 0.05$). Similarly, size class had a significant effect on the proportion of body contacts ($\chi^2 = 29.2$, df = 2, $p = 4.6 \times 10^{-7}$), with large individuals contacting the screens significantly fewer times with their tails (resulting in a greater proportion of body contacts) than both small- ($p = 0.005$) and intermediate-sized fish ($p = 5.4 \times 10^{-5}$). Finally, size class did not have a significant effect on the proportion of time spent near screens ($\chi^2 = 4.88$, df = 2, $p = 0.09$), with all fish spending a greater proportion of the trial upstream of screens than near them (proportion of <0.5).

To further examine the relationship of size (FL) on fish behavior, GLMs of the continuous variable of FL were analyzed for each response variable. For total screen contacts (log transformed) and the proportion of time spent near screens, the best-fitting model was found to be a linear regression between FL and the response variable ($y = 1.13 - 0.012 \times FL$; $y = -0.35 - 0.023 \times FL$, respectively.). However, FL did not significantly affect the total number of screen contacts ($F^{1,63} = 0.47$, $p = 0.49$) or the proportion of time spent near screens ($F^{1,63} = 0.95$, $p = 0.33$).

The size of individuals significantly affected the proportion of body contacts ($F_{1,59} = 12.25$, $p = 0.0009$). The significant relationship between FL and the proportion of body contacts was described by the logistic equation: $y = 2.05 - 0.39 \times FL + 0.01 \times FL^2$ (Fig. 2).

Discussion and conclusions

Overall, we show that fish size is an important determinant of how juvenile green sturgeon behave near fish-exclusion screens, and is an important consideration for how these fish may be interacting with anthropogenic devices in natural systems. As fork length increased for small and

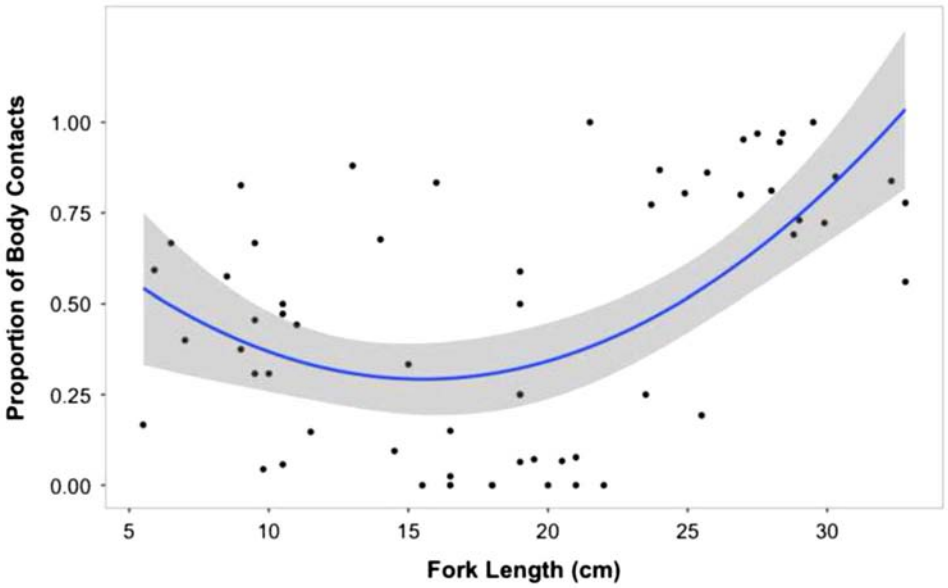

Fig. 2. The best-fit line for the change in the proportion of body contacts relative to size (fork length). The significant relationship (p = 0.0009) between proportion of body contacts and size was found to be: $y = 2.05 - 0.39 \times FL + 0.01 \times FL^2$. The shaded area represents the 95% confidence interval for the line.

intermediate stage juveniles, the most significant effect was a reduction in the proportion of screen contacts that were made by the body of the fish as opposed to the tail. While the use of sensory deterrents slightly, though not significantly, decreased the number of times fish contacted the screens for small juveniles, a similar effect on the behavior of intermediate juveniles was not seen.

Small- and intermediate-sized sturgeon differed in the proportion of times they contacted the screens with their body, likely representing a change in their rheotactic behavior as opposed to a direct result of the absolute size differences. Although we did not quantify rheotaxis directly, the proportion of body contacts is a proxy for orientation relative to the current, since the way in which fish contacted screens is due largely to their angle of approach. Fish that were positively rheotactic as they moved downstream were more likely to contact the screens with their tails, while negatively rheotactic fish were more likely to contact screens with their bodies. This could be an indication of a change in movement behavior as fish undergo ontogenetic development. It is possible that the differences in the proportion of body contacts seen among size classes could indicate a rheotactic preference that is correlated with dispersal patterns.

When compared with larger fish, analysis of the proportion of body contacts against fork length revealed another distinct change in the behavior of fish, such that larger fish behaved differently than the early and intermediate juveniles tested here (Fig. 2; Table 2). Under control conditions, larger fish contacted the screens more often with their bodies compared to the other size classes, with body contacts occurring 83% of the time (0.83 ± 0.03).

Analyses revealed that this change in behavior occurred somewhere between roughly 18 and 20 cm in fork length (Fig. 2), indicating this to be an important transitional life stage for juvenile green sturgeon. This stage correlates with the size of fish at which green sturgeon are able to tolerate transition to full-strength saltwater (Allen and Cech 2007; Allen et al. 2009). The change in behavior observed in our data likely reflects the morphological, behavioral, and physiological changes underpinning the "pseudo-smoltification" of green sturgeon, in which fish begin to remodel their physiology in preparation for the osmoregulatory demands that accompany living in brackish and salt water (Allen et al. 2011). While fish are undergoing this preparation for increased salinity, it is possible that an energetic trade-off between the physiological changes and other measures, such as swimming performance, may exist. Indeed, Allen et al. (2006) found that as size increased in green sturgeon that were saltwater tolerant, there was a corresponding decrease in their critical swimming velocity (U_{crit}). This decrease in U_{crit} was seasonal, and older fish of the same size did not exhibit this negative relationship between size and U_{crit}. Many of the seawater tolerant fish tested by Allen et al. (2006; 26 – 47 cm total length) were similar in size and age to the stage at which the change in behavior was observed here (i.e., 20 cm in fork length approximates 25-26 cm in total length for juvenile green sturgeon). Additionally, as juvenile green sturgeon approach the size at which they are able to tolerate seawater, a change in rheotactic preference also likely occurs. Intermediate-sized juveniles that have not yet undergone a transition to saltwater tolerance remain further upstream in rearing and foraging grounds, and a preference for positive rheotaxis may facilitate this upstream position. Our data support this idea, since many intermediate-sized fish between ca. 15–20 cm in length exhibited low proportions of body contacts (a proxy for rheotaxis). As juveniles grow and age, this preference for positive rheotaxis may disappear until juveniles that are of the size and age to migrate actively may move downstream with negative rheotaxis. Our data support this generalized ontogenetic model, since the proportion of body contacts increased as fish increased in size and age from intermediate- to large-sized juveniles. Therefore, the way

in which juvenile green sturgeon approached the fish screens continuously changed as they grew in size.

This is consistent with previous work on juvenile green sturgeon that quantified rheotactic behavior in the laboratory as fish developed. Kynard et al. (2005) found that juveniles aged 110–181 dph exhibited increased downstream movement behavior during nocturnal hours, with peaks in downstream movement in subsequent experimental seasons occurring at 153-154 and 171 dph, respectively. These age ranges are similar to those that were compared in the previous and current studies, and the increase in downstream movement found by Kynard et al. (2005) is consistent with the increase in negative rheotaxis (expressed as an increase in the proportion of body contacts) documented in fish in our studies. Similarly, Boys et al. (2013b) found that an assemblage of freshwater fish species in Australia were significantly more likely to make contact with a fish screen when orienting with negative rheotaxis, underscoring the importance of including considerations of migratory behavior and physiology in inland fisheries management.

The proportion of body to tail contacts may also influence the relative impact of each type of interaction. For example, contacts with the screen by the body of the fish could be potentially more injurious, since a greater surface area of body tissue comes into contact with the screen relative to the tail. Similarly, due to a greater area in contact with screen faces, body contacts might result in more impingements compared to tail contacts, though this has not been analyzed in previous studies, and we were not able to quantify this due to the low number of impingements observed. The specific physical and physiological impact of each type of screen contact should be further investigated in future studies.

The sensory deterrent treatments tested in this study not did significantly affect any of the behavioral indices quantified for small or intermediate-sized fish, which is consistent with previous laboratory studies of sensory deterrents and juvenile green sturgeon behavior (Poletto et al. 2014a). Among other fishes, however, evaluations of the efficacy of behavioral sensory deterrents have been equivocal, with results having various levels of success depending on the species tested and the environmental context in which the sensory stimulus was presented. For example, while acoustic vibrations successfully repelled Atlantic herring (*Clupea harengus*), a similar result was not found for three-spine stickleback (*Gasterosteus aculeatus*; Maes et al. 2004). Similarly, when used in low velocity conditions, strobe lights effectively deterred juvenile salmonids (Johnson et al. 2005), but this avoidance response was greatly attenuated in other species as water velocity increased (Sager et al. 2000). Continued anthropogenic modification of riverine habitats requires

effective management and conservation practices for inland fishes, but we emphasize that care should be taken when developing management strategies that include the use of sensory deterrents. Our data, combined with previous literature showing the mixed success of sensory deterrents, highlight the importance of laboratory testing prior to field implementation, and demonstrate the need to consider the often context- and species-specific sensory responses of fishes when determining the most effective means of mitigation for water diversions.

While water diversions are prevalent throughout the watershed in which green sturgeon live and likely pose a risk to all early life history stages (Mussen et al. 2014; Poletto et al. 2014a, 2015), our work suggests that ontogeny may play a significant role in how susceptible juvenile green sturgeon are to injury or mortality from fish-protection devices. Somewhat paradoxically, larger, older juveniles that are capable of outmigrating may be more susceptible to interactions with fish protection devices such as fish screens, and therefore could be an important life history stage for targeted management and conservation actions. Migrating juveniles are at risk not only due to their reduced swimming capabilities, but also due to their presumed heightened probability of repeated interactions with fish screens. Managers seeking to reduce the potentially harmful effects of water diversions fitted with fish screens could limit intake velocities at these structures to match the U_{crit} of larger, migrating juveniles during the time of year at which these migrations occur. This has been previously suggested for both larval green and white sturgeon (Verhille et al. 2014), and may be an important mechanism to balance water diversion activities with conservation actions by limiting intake velocities during critical seasonal and ontogenetic periods. By focusing conservation and management efforts on juvenile green sturgeon at the greatest risk, managers can therefore improve the efficiency and impact of mitigation.

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